Daytime Vertical Distribution of Microzooplankton in the Hawkesbury-Nepean River

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Daytime vertical distribution of 18 dominant taxa of freshwater microzooplankton was examined in mid-channel open water at North Richmond in the Hawkesbury-Nepean River, New South Wales, by measuring their densities at two depths about biweekly throughout the year. The objective was to test whether or not there was any significant depth-related distributional pattern for the dominant microzooplankton. Ten taxa were heterogeneously distributed with depth over the sampling period. Among the taxa that exhibited vertical heterogeneity, rotifers were distributed more abundantly either near the surface or in the deeper water, whereas microcrustaceans were distributed more abundantly in the deeper water. The observed vertical distributional patterns appeared to be largely independent of river flow rate. For the estimate of density of zooplankton in the water column, depth-integrated collection of quantitative samples may generally be recommended even in rivers to reduce sampling bias deriving from the likely heterogeneous distribution of river zooplankton with depth.

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INTRODUCTION

Zooplankton may be heterogeneously distributed with depth in lakes. They may exhibit a discernible diel vertical migration (Kikuchi 1930; Zaret and Suffern 1976; Bayly 1986; Lampert 1989). In this migration, crustacean zooplankton such as large daphnids and calanoid copepods are distributed in the deeper water during the day, although there are exceptions to such a pattern (Bayly 1986).

The densities of microzooplankton may also exhibit marked vertical heterogeneity. For example, species of the rotifers *Keratella*, *Kellicottia* and *Polyarthra* are perennially surface water forms whereas species of *Synchaeta* and *Collotheca* are found mainly in the upper layer during summer but populate deeper water during autumn in a Norwegian lake (Larsson 1971). Similarly, the rotifers *Keratella cochlearis* Gosse and *Filinia brachiata* (Rousselet) mostly occupy an upper layer in a shallow English tarn during the day (Stewart and George 1988). On the other hand, the small planktonic cladoceran *Bosmina longirostris* (O.F. Müller) and nauplii are distributed near the bottom in shallow Canadian shield lakes during the day (Schindler and Novén 1971). Nauplii and copepodites of *Pseudodiaptomus* also are found near the bottom during the day in a subtropical lake in southern Africa (Hart and Allanson 1976).

In contrast to many reported patterns in the vertical distribution of lake zooplankton, little is known of the distribution in rivers. This is because in rivers, zooplankton samples are often collected at a single depth (e.g. Vásquez and Rey 1989; Thorp et al. 1994), with the assumption of uniform distribution of zooplankton with depth in rivers where the waters are presumably well mixed because of dispersion and turbulence, compared with those in lakes (Pace et al. 1992). Even when zooplankton samples are collected at different depths, the samples are combined for the depth-integrated estimate of density (e.g. Neitzel et al. 1982; Guisande and Toja 1988).

However, Brook and Rzòska (1954) report the heterogeneous distribution of dominant crustacean zooplankton species in the White Nile, by estimating the densities of these zooplankters at three depths at 15 locations. They note that the density maxima occurred at the surface for most of the zooplankton species examined, although their observation was not temporally replicated. Also, Shiel et al. (1982) dispute the assumption of uniform distribution of river zooplankton. They have described heterogeneity in both horizontal and vertical quantitative samples from the Murray River, South Australia.

Vertical distribution of zooplankton may have important ecological implications in aquatic systems, especially in relation to the spatial variability of intensity of grazing and the pattern of nutrient regeneration by zooplankton in the water column (Angeli et al. 1995 and references therein; Kobayashi et al. 1996). In the present study, daytime vertical distribution of dominant microzooplankton taxa was examined in mid-channel open water at North Richmond, by measuring their densities about biweekly at two depths throughout the year. The objectives of the present study were to determine 1) if there was any significant difference in the density of dominant river microzooplankton between depths over the sampling period and 2) if there was any significant correlation between the river flow rate and vertical distributional pattern of the dominant river microzooplankton.

MATERIALS AND METHODS

Study Site

The study site (approximately 33°40′S, 150°40′E) is located at North Richmond, about 140 km upstream of the mouth of the Hawkesbury-Nepean River, New South Wales (length of main river channel: approximately 300 km; total catchment area: 22,000 km^2) (see Fig. 1 in Kobayashi et al. 1996). Five dams and more than 13 weirs on the main river channel regulate the river flow. The study site is in the upper tidal freshwater portion of the river, about 6 m deep and 120 m wide. Data on flow rate ($l\ s^{-1}$) over Penrith weir (the closest non-tidal gauging station to North Richmond) were provided by AWT Hydrographic Services. River flow rate varied in the range 377–14,142 $l\ s^{-1}$ during the study period of May 1992 to April 1993 (see Fig. 2 in Kobayashi et al. 1996).

Zooplankton Collection, Sampling and Counting

From May 1992 to April 1993, four replicate samples of zooplankton were collected about biweekly at each depth of 1 m and 4 m in mid-channel open water, with the aid of a 4.2–l Haney-type trap (Gawler and Chappuis 1987). Sampling was conducted between 1000 and 1400 h and took ~30 min to collect and filter a total of eight zooplankton samples on each sampling date. Zooplankton specimens were filtered in the field through a 35 μm mesh netting (Likens and Gilbert 1970) and preserved with a 4% buffered sugar-formaldehyde solution (Haney and Hall 1973). Further details are described in Kobayashi et al. (1996).

A 1ml width-mouth automatic pipette and a Sedgwick-Rafter counting chamber were used for subsampling and counting of zooplankton. Zooplankton was identified and counted under an inverted microscope at magnifications of x25 to x100. Preliminary counting of 5 replicate samples established that the coefficient of variation was reduced to ~0.1 when the mean number of the specimens counted exceeded 80. Therefore, the subsampling and counting were repeated until a minimum of 80 specimens of the most abundant taxon were counted. Counts included all zooplankters except protists for which testate amoebae and ciliates were counted. Zooplankton was identified by reference to the relevant taxonomic literature (primarily Koste 1978; Smirnov and Timms 1983; Koste and Shiel 1987; Bayly 1992).

In the present study, dominant zooplankton taxa were arbitrarily defined as those present in more than 50% of the total samples (total n=23), with an added mean density at depths of 1 m and 4 m exceeding 20 animals l^{-1} in at least one sample.

TABLE 1

Comparison of overall mean density of dominant zooplankton taxa between 1 m and 4 m depths at North Richmond. Overall mean density: arithmetic mean values and mean log values in parentheses are shown. Logarithmic transformation was $\log_{10}$ (animals+0.1). Log-transformed values were used for overall density comparison. Type of test performed: T, two-sample *t* test (two tailed) if there was no significant correlation in mean densities between the two depths; PT, paired-sample *t* test (two tailed) if there was a significant correlation in mean densities between the two depths. n is the sample size and p is the significance level.

Taxon	n	Overall mean density (animals l^{-1}) 1 m	4 m	p	Test
a) Mean density at 1 m > mean density at 4 m					
Polyarthra spp. (chiefly *P. dolichoptera* Idenlson)	23	635.5(2.005)	139.1(1.528)	0.0047	PT
Proalides tentaculatus De Beauchamp	15	35.3(0.716)	15.1(0.328)	0.0101	PT
Synchaeta spp. (chiefly *S. pectinata* Ehrenberg)	23	113.4(1.725)	86.3(1.408)	0.0319	PT
Trichocerca spp.	23	29.4(1.137)	12.1(0.662)	0.0121	T
b) Mean density at 1 m is not significantly different from mean density at 4 m					
Ciliates	23	45.5(1.312)	29.4(1.143)	0.0636	PT
Asplanchna spp. (chiefly *A. priodonta* Gosse)	21	33.8(0.384)	5.7(0.163)	0.2385	PT
Brachionus angularis Gosse	17	76.7(1.261)	59.1(1.115)	0.3990	PT
Brachionus calyciflorus Pallas (long-spined form)	13	7.3(0.246)	10.3(0.323)	0.6579	PT
Conochilus dossuarius Hudson	23	64.6(0.879)	75.6(1.082)	0.1170	PT
Filinia spp. (chiefly *F. longiseta* Ehrenberg)	22	21.7(0.113)	5.4(–0.016)	0.3868	PT
Keratella cochlearis (Gosse)	23	37.5(0.593)	23.6(0.858)	0.1615	PT
Keratella tropica (Apstein)	14	4.6(–0.207)	12.5(0.463)	0.0607	T
c) Mean density at 1 m < mean density at 4 m					
Brachionus calyciflorus (short-spined form)	12	1.0(-0.665)	6.7(0.016)	0.0117	T
Bosmina meridionalis Sars	14	0.3(-0.882)	3.4(–0.169)	0.0018	T
Hexarthra spp. (chiefly *H. intermedia* Wiszniewski)	17	76.2(0.589)	88.4(1.158)	0.0487	PT
Keratella procurva (Thorpe)	18	3.2(–0.450)	7.3(0.084)	0.0035	PT
Nauplii	23	37.9(0.877)	81.7(1.267)	0.0056	PT
Copepodites	21	4.6(–0.388)	21.1(0.574)	0.0011	T

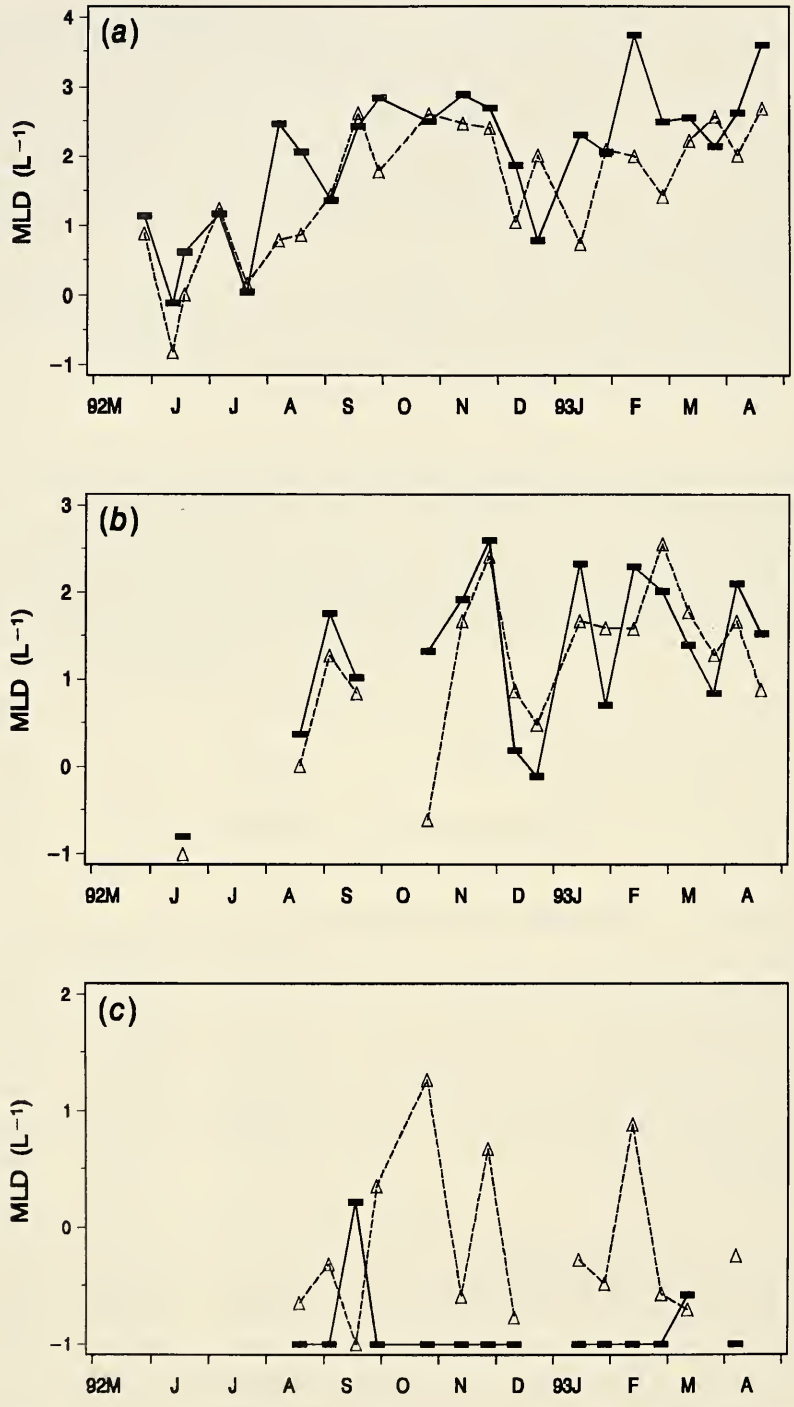

Figure 1. Examples of seasonal pattern in vertical distribution of zooplankton at North Richmond. Mean log density (MLD: $\log_{10}$ (animals+0.1) l^{-1}) is shown on each sampling date (n=3–4 on each sampling date). ■ MLD at 1m; △ MLD at 4 m. (a) *Polyarthra* spp.; (b) *Brachionus angularis*; (c) *Bosmina meridionalis*.

Statistical Analyses

Prior to analysis, density data were transformed by $\log_{10}(x+0.1)$ to stabilise the variance. The constant of 0.1 added corresponds to the lowest density value possible in the sampling and counting procedures used in the present study. The addition of the constant was necessary because some of the density values were zero. The mean log-densities of zooplankton were then calculated for each taxon at depths of 1 m and 4 m, respectively, on each sampling date. For the zooplankton taxa for which the pairwise mean log-densities were seasonally and significantly correlated between depths (Pearson product-moment correlation, $\alpha=0.05$), paired-sample *t* test (two-tailed) was applied to test the null hypothesis that the mean density difference equaled zero between the two depths over the sampling period ($\alpha=0.05$). For the zooplankton taxa for which there was no significant correlation between the pairwise mean log-densities at depths of 1 m and 4 m over the sampling period, two-sample *t* test (two-tailed) was used to test the null hypothesis. The paired-sample *t* test is more powerful than the two-sample *t* test, if there is pairwise correlation of data from the two samples. If no such correlation exists, then two-sample *t* test is the more powerful procedure (cf. Zar 1984:152).

In addition, relative density at 1 m depth (RD_{1m}, %) was estimated for each taxon on each sampling date when animal density at 1 m or 4 m >0:

RD_{1m}=(density at 1 m)/[(density at 1m)+(density at 4 m)] x 100

Spearman's rank correlation analysis was used to test if there was any significant correlation between river flow rate and the RD_{1m} for each microzooplankton taxon.

All analyses were performed using the SAS (Anon. 1989) computer programs.

RESULTS

Overall Difference in Density Between the Two Depths

A total of 18 dominant microzooplankton taxa were examined (Table 1). Seven taxa (*Polyarthra* spp., *Synchaeta* spp., *Trichocerca* spp., nauplii, ciliates, *C. dossuarius* and *K. cochlearis*) occurred throughout the study, whereas the remaining taxa were seasonal. The mean densities of microzooplankton temporarily fluctuated at both depths, but tended to correlate between the two depths (Fig. 1). A maximum mean density of 5,748 animals l^{-1} (mean $\log_{10}(x+0.1)$-density: 3.735) was recorded for *Polyarthra* spp. (chiefly *P. dolichoptera*) at a depth of 1m on 12 February 1993.

Over the sampling period, the null hypothesis was rejected for ten taxa, indicating that there was a significant difference in their overall mean densities between the two depths (Table 1). Of these, the overall mean densities of *Polyarthra* spp., *P. tentaculatus*, *Synchaeta* spp. and *Trichocerca* spp. were significantly greater at 1 m depth than at 4 m depth (Fig. 2a). On the other hand, the overall mean densities of *B. calyciflorus* (short-spined form), *K. procurva*, *Hexarthra* spp., *B. meridionalis*, nauplii and copepodites were greater at 4 m depth than at 1 m depth at North Richmond (Fig. 2c). The null hypothesis was not rejected for the remaining eight microzooplankton taxa examined, indicating that there was no significant difference in their overall mean densities between the two depths over the sampling period (Fig. 2b). Note that this does not necessarily imply that their mean densities were the same at the two depths on each sampling date.

Spearman's Rank Correlation of RD1m With River Flow Rate

On a taxon-specific basis, there was a significant negative correlation between river flow rate and RD_{1m} for the rotifers *Asplanchna* spp. and *B. angularis* (Fig. 3). An overall plot of the RD_{1m} for the examined microzooplankton against river flow at North Richmond showed no significant correlation between them (Fig. 4).

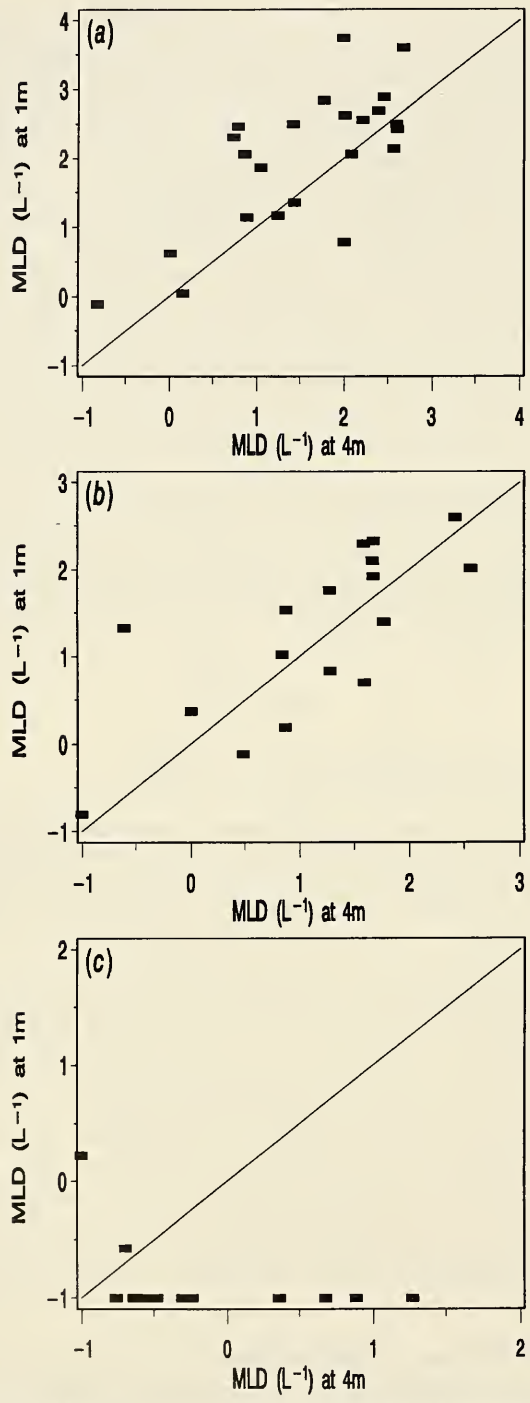

Figure 2. Examples of overall pattern in vertical distribution of zooplankton at North Richmond. Mean log density (MLD: $\log_{10}$ (animals+0.1) l^{-1}) at 1 m is plotted against MLD at 4 m. (a) *Polyarthra* spp. (overall MLD at 1 m > overall MLD at 4 m); (b) *Brachionus angularis* (overall MLD at 1 m is not significantly different from overall MLD at 4 m); (c) *Bosmina meridionalis* (overall MLD at 1 m < overall MLD at 4 m).

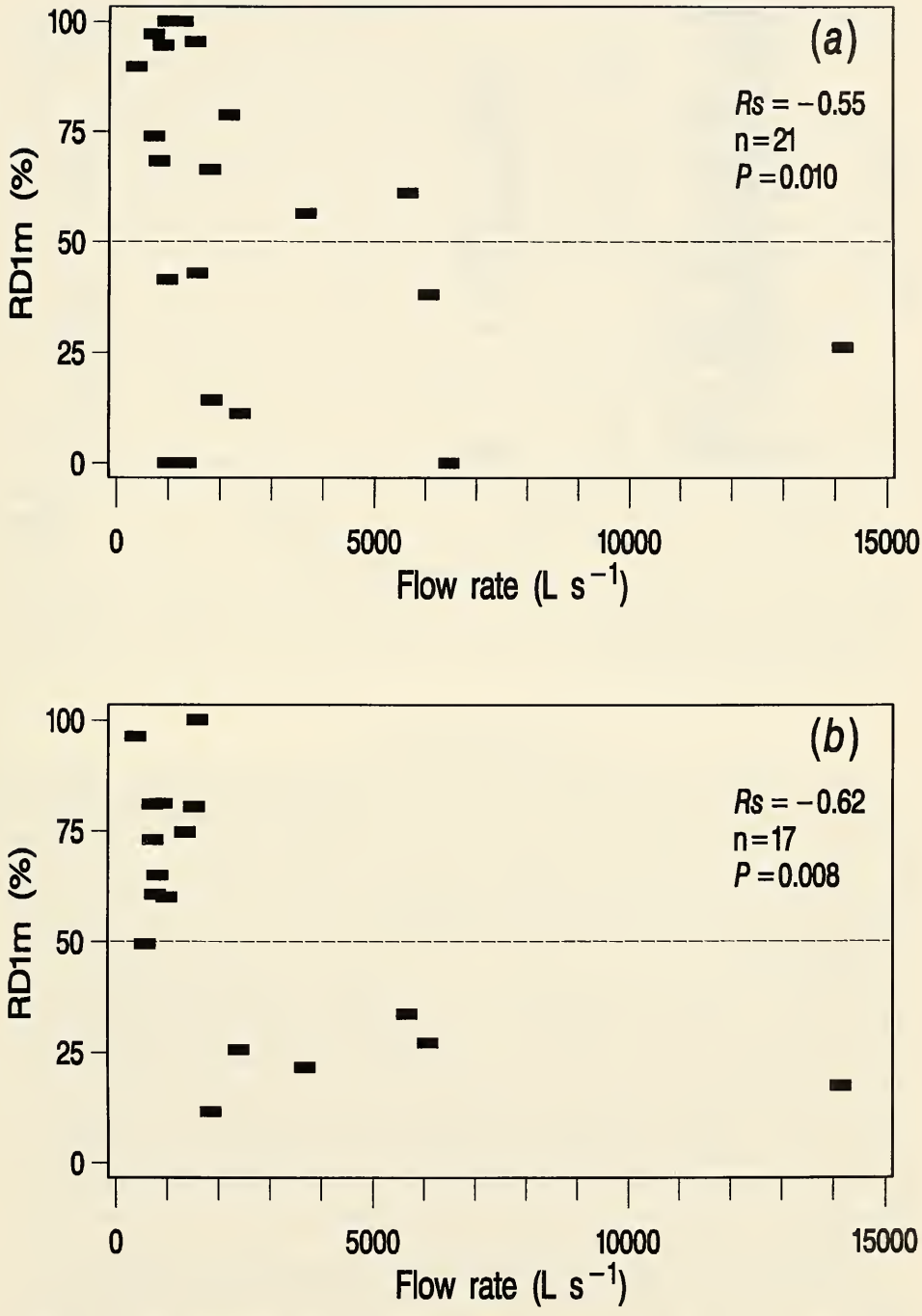

Figure 3. Significant correlation of relative densities at a depth of 1 m (RD_{1m}, %) with river flow rate at North Richmond (flow rate was measured at the gauging station over Penrith weir: see Fig. 1 in Kobayashi et al. 1996 for location of the gauging station): (a) *Asplanchna* spp., (b) *Brachionus angularis*. R_S, Spearman's rank correlation coefficient; n, sample size and p, significance level.

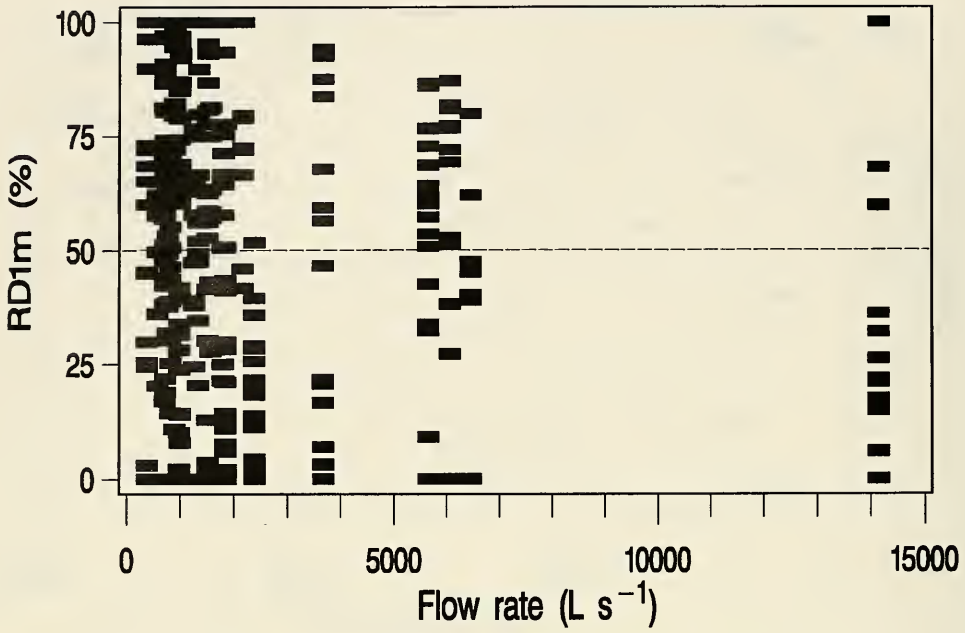

Figure 4. Overall relationship between river flow rate and relative densities at a depth of 1 m (RD_{1m}) for microzooplankton at North Richmond.

DISCUSSION

The dominant microzooplankton taxa were not necessarily uniformly distributed with depth at the studied site of North Richmond. Rotifers showed species-specific patterns in the vertical distribution, with some taxa being distributed more abundantly near the surface and the others in the deeper water. The microcrustaceans were distributed more abundantly in the deeper water. For some taxa, especially ciliates, the pooling of density may have masked possible species-specific patterns in the vertical distribution in the present study.

It is difficult to speculate whether or not the observed overall heterogeneous distribution of some of the microzooplankton taxa with depth is common in freshwater rivers because there seem to be no comparative data available from similar freshwater systems in the literature. Compared to lake microzooplankton, the surface water occurrence of *Polyarthra* spp. and the deeper water occurrence of *B. meridionalis* and juvenile copepods at North Richmond are consistent with the patterns reported for the congeneric taxa in some of the Northern and Southern Hemisphere lakes (Larsson 1971; Schindler and Novén 1971; Dumont 1972; Hart and Allanson 1976). However, the absence of consistent vertical distributional patterns for *Asplanchna* spp., *K. cochlearis* and *Filinia* spp. at North Richmond differs from the surface water occurrence of these taxa reported elsewhere (Dumont 1972; Stewart and George 1988).

The studies of the vertical distribution of microzooplankton in lakes indicate that the vertical heterogeneity of microzooplankton is often observed but the patterns of such a distribution can exhibit taxonomic variation and also temporal and spatial variation for the same taxa (Kikuchi 1930; George and Fernando 1970; Stewart and George 1988). The variability in the vertical distribution of microzooplankton may also be expected for rivers. Further inter-river comparison is necessary to verify this assertion. Nevertheless, in addi-

tion to reported horizontal (longitudinal) heterogeneity (e.g. Basu and Pick 1997; Pourriot et al. 1997), the vertical heterogeneity of river zooplankton suggests that even in rivers, depth-integrated collection of quantitative samples may generally be recommended to estimate the density of zooplankton in the water column (Brook and Rzòska 1954).

In running waters, the degree of turbulence usually increases as the mean velocity of the flow increases so one would expect greater mixing at greater flow rates. This suggests that, as a general trend, the RD_{1m} for river mirozooplankton may converge to 50% with increasing flow rate, if the vertical positions of the microzooplankton are passively determined by the degree of mixing proportional to river flow rate. An overall scatter plot of the RD_{1m} for the examined microzooplankton against river flow at North Richmond shows that this was not the case within the observed flow range in this study. On a taxon-specific basis, the RD_{1m} of two rotifer taxa were negatively correlated with river flow. These results indicate that the relative vertical distribution of dominant microzooplankton at North Richmond may largely be independent of river flow rate.

In the present study, the diel variation in the vertical distribution of microzooplankton was not investigated. For rivers, Shiel et al. (1982) conducted a 24–h study of changes in species composition and density of mid-channel winter plankton, by collecting hourly samples at a freshwater site at a depth of 3 m in the Murray River in South Australia. For the zooplankton, they noted little change in species composition overall, but a distinct change in density. They recorded a minimum of less than 20 animals l^{-1} around midnight and a maximum of 993 animals l^{-1} at dusk. Although in their diel study, the plankton samples were collected at a single depth, such temporal variation in density may partly reflect diel vertical movement of river microzooplankton. Further study is warranted to examine whether the observed patterns in the daytime vertical distribution of the dominant microzooplankton differ at night in the Hawkesbury-Nepean River.

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